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Research Article

When Are Attention and Saccade Preparation Dissociated?

Artem V. Belopolsky and Jan Theeuwes

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ABSTRACT—*To understand the mechanisms of visual attention, it is crucial to know the relationship between attention and saccades. Some theories propose a close relationship, whereas others view the attention and saccade systems as completely independent. One possible way to resolve this controversy is to distinguish between the maintenance and shifting of attention. The present study used a novel paradigm that allowed simultaneous measurement of attentional allocation and saccade preparation. Saccades toward the location where attention was maintained were either facilitated or suppressed depending on the probability of making a saccade to that location and the match between the attended location and the saccade location on the previous trial. Shifting attention to another location was always associated with saccade facilitation. The findings provide a new view, demonstrating that the maintenance of attention and shifting of attention differ in their relationship to the oculomotor system.*

Saccadic eye movements are necessary to quickly build an accurate representation of the visual environment, as they bring the fovea, the part of the retina with the highest acuity, to objects of interest. Because of this physiological aspect of the visual system, visual selection becomes, by definition, an active, overt process (Findlay & Gilchrist, 2003). However, it is also known that humans are able to allocate visual attention without shifting gaze. These covert attentional shifts result in enhanced processing at the attended location, which can be measured on both behavioral and neural levels (Mangun et al., 2001; Posner, 1980). Knowing the relationship between these two types of orienting is crucial for understanding the function and mechanisms of spatial attention (for a review, see Awh, Armstrong, & Moore, 2006).

According to one view, spatial attention constitutes a high-level, supramodal cognitive function that interacts with the low-

level, specialized sensory and motor processing systems only for the purpose of input and output and that can be functionally distinguished from them (Hunt & Kingstone, 2003b; Klein, 1980; Klein & Pontefract, 1994; Posner & Petersen, 1990). Alternatively, spatial attention can be viewed as a direct product of these low-level processing systems and, more specifically, as a product of active interactions with the environment through eye movements (Smith, Rorden, & Jackson, 2004). The influential premotor theory (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Rizzolatti, Riggio, & Sheliga, 1994) posits that a shift of spatial attention involves all the steps necessary for making a saccade, except for the actual motor execution (see also Klein, 1980; Klein & Pontefract, 1994).

Such “grounding” of spatial attention in the oculomotor system would predict an interdependent relationship between covert and overt attentional orienting, such that a factor that affects one should necessarily affect the other. Indeed, there is a great deal of experimental evidence indicating a close link between the covert-attention and oculomotor systems. Behavioral studies have shown that allocation of attention affects saccade trajectories (Sheliga, Riggio, & Rizzolatti, 1995; Van der Stigchel & Theeuwes, 2007), have demonstrated a coupling between saccade preparation and spatial attention (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995; Shepherd, Findlay, & Hockey, 1986), and have shown that the ability to make eye movements can affect covert attention (Craighero, Nascimben, & Fadiga, 2004; Smith et al., 2004). In addition, neurophysiological studies have shown that subthreshold stimulation of several oculomotor structures, such as the frontal eye fields (FEF) and superior colliculus (SC), results in enhanced visual sensitivity at the corresponding retinotopic location (Cavanaugh & Wurtz, 2004; Moore & Fallah, 2001, 2004; Muller, Philastides, & Newsome, 2005).

However, if attention is an independent supramodal system, a functional dissociation between attention and eye movements should be observed. Studies supporting this idea have shown that some neurons within FEF and SC (visuomotor neurons) follow the movements of attention, whereas other neurons (pure

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motor neurons) either are not modulated or are even inhibited during shifts of covert attention (Ignashchenkova, Dicke, Haar-meier, & Thier, 2004; Juan, Shorter-Jacobi, & Schall, 2004; Thompson, Biscoe, & Sato, 2005). Moreover, several behavioral studies using a dual-task design showed that saccade preparation does not result in enhancement of target detection at the location of the prepared saccade, and that maintaining attention does not facilitate initiation of a saccade to the attended location (Hunt & Kingstone, 2003a; Klein, 1980; Klein & Pontefract, 1994).

In this article, we provide evidence that this controversy can be resolved if a distinction is made between the maintenance of attention at a location and the shifting of attention to a location. We designed a task that allowed simultaneous measurement of attentional allocation and saccade preparation, avoiding the typical problems of prioritizing one task over the other that are associated with the dual-task designs (Pashler, 1989). Our task did not create competition between covert and overt shifting of attention, as dual-task paradigms usually do. In our task, covert attention needed to be shifted to identify a target character, and then a saccade had to be prepared and executed to one of two

locations, as determined by the identity of the target (either 1 or 2).

It is known that certain classes of stimuli (such as luminance changes) directly affect both attention and eye movement systems (Abrams & Dobkin, 1994). In the study reported here, we focused only on voluntary shifts of attention. We report data from two experiments, which differed only in the probability that a saccade had to be executed to the location to which covert attention was already allocated. In addition, the dynamics of the coupling between covert attention and saccade preparation were examined by analyzing effects across consecutive trials.

EXPERIMENT 1

As noted, we used a task in which attentional allocation and saccade preparation were measured simultaneously. Attentional allocation was measured using a modification of the classic Posner cuing task (see Fig. 1). Participants had to covertly shift their attention according to a central pointer cue, which indicated where (out of two possible locations) the target was likely to appear (i.e., the target appeared in the cued location on 80%

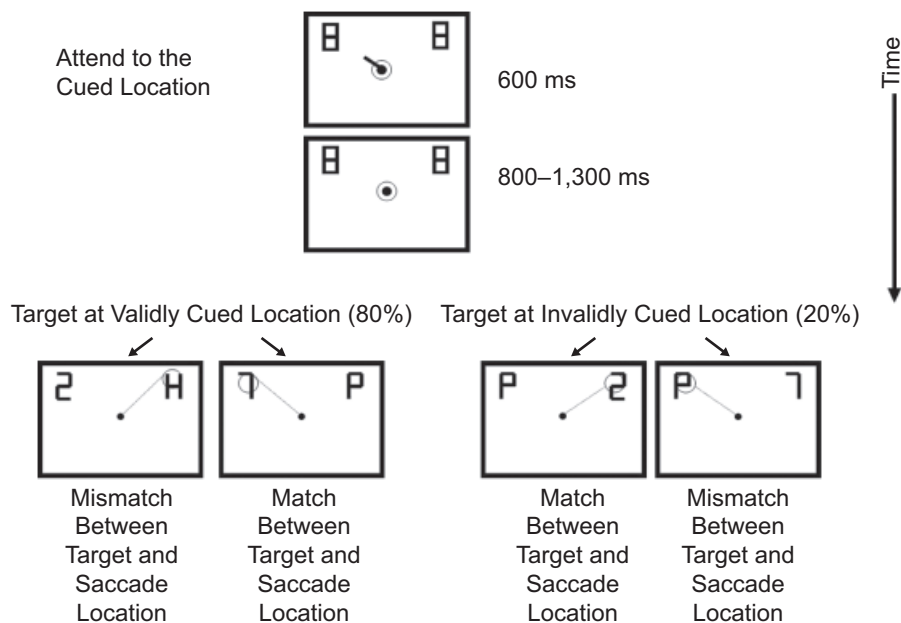


Fig. 1. Illustration of the events on a typical trial in Experiment 1. Initially, two figure-eight pre-masks were displayed, and participants had to direct covert attention (not their eyes) to the location indicated by the central pointer (in this example, the upper left location). Then, after a variable interval, characters were revealed by removing line segments from the pre-masks. Participants had to identify the target (1 or 2), which was presented either at the location to which attention was directed (validly cued trial; two examples on the left) or at the location to which attention was not directed (invalidly cued trial; two examples on the right). Depending on the identity of the target, participants had to make a saccade to one location or the other: 1 meant that a saccade should be made to the left location, and 2 meant that a saccade should be made to the right location. (Saccades are illustrated by a thin line and a circle.) Note that in the match condition, the target indicated that a saccade had to be made to the same location at which covert attention was allocated (in order to identify the digit); in the mismatch condition, the target indicated that a saccade had to be made to the other location. In Experiment 2, two symmetric locations were added to the lower hemifield, and the targets were numbers 1, 2, 3, and 4. (Note that because of the figure-eight pre-masks, the digit 1 looked very much like a 7. Participants were informed that the digit was in fact 1.)

of the trials). Depending on the identity of the target (either 1 or 2), participants then had to make a saccade to one or the other location. We expected the classic Posner-like cuing effect: shorter saccadic reaction time (SRT) on validly cued trials (in which attention was allocated to the location where the target character subsequently appeared) than on invalidly cued trials (in which the target character appeared at the location that was not initially cued).

To measure saccade preparation, we asked participants to make an eye movement to a location indicated by the target's identity. Specifically, depending on the target's identity, they were required to shift their gaze to one of the two locations, and this saccade could be either toward (match trial) or away from (mismatch trial) the target's location. Note that voluntary saccade preparation could start only after the target was identified. Critically, there was no advantage to preparing a voluntary eye movement to a specific location, because saccades to the two locations in the display were equally likely. Given that there was no probability incentive, no voluntary saccade preparation was expected.

In both the validly and invalidly cued trials, covert attention had to be allocated to the target location in order for the participant to identify the target character (either 1 or 2). If, as predicted by the premotor theory, the allocation of covert attention implies the preparation of a saccade, then the identification of the target should have implied the preparation of a saccade to that location. In this case, saccades to the target location (match trials) would be expected to be initiated faster than saccades to the non-target location (mismatch trials). However, if covert attention is an independent mechanism, the preallocation of covert attention (necessary for target identification) would not be expected to have any benefit for saccade initiation. In this case, saccade preparation would start in the same way on match and mismatch trials, and no difference in SRT between match and mismatch trials would be expected.

On both validly and invalidly cued trials, covert attention had to be allocated to the target's location, but in the former case, attention was already there before the target appeared, whereas in the latter case, attention had to be shifted to the target location. To determine whether the maintenance and shifting components of attention differ in their relationship to the oculomotor system, we compared saccade preparation on validly cued trials (in which attention had to be maintained at the cued location) with saccade preparation on invalidly cued trials (in which attention had to be shifted to a new location in order to process the target). An interaction between cue validity and saccade location (match vs. mismatch) would indicate that the acts of maintaining and shifting attention differ in their reliance on the oculomotor system.

Method

All stimuli were presented on a computer screen. Each trial began with a display of two figure-eight premasks ($1^\circ \times 1.5^\circ$, 58

cd^{-2}) on a black background; the premasks were presented in the upper hemifield 5.7° from the fixation point and 8° from each other. After 500 ms, a central pointer appeared at fixation for 600 ms; this cue indicated which of the two premask locations was the location where the target was likely to appear (i.e., with 80% probability; see Fig. 1). After a random interval of 800 to 1,300 ms, line segments of the figure-eight premasks were removed, revealing the target (a number) and a distractor (a letter) for 2,000 ms. The target could be either the number 1 or the number 2, and the distractor could be either the letter H or the letter P. Participants had to detect and process the target character and make a saccade to the appropriate location: The target 1 indicated that the saccade had to be made to the location on the left, whereas the target 2 indicated that the saccade had to be made to the location on the right. The factors of target location and saccade endpoint were manipulated orthogonally (see Fig. 1 for all possible combinations). Thus, the probability that the target and saccade locations coincided was 50%. Eye movements were recorded with an EyeLink Tracker (500-Hz temporal resolution, 0.2° spatial resolution). Ten naive participants completed two practice and eight experimental blocks of 40 trials each.

Results and Discussion

Trials with saccades faster than 80 ms or slower than 1,100 ms and trials with saccades that did not start within 1° of the fixation point were discarded from further analyses. This resulted in an average loss of 9% of trials. One participant was replaced because of excessive errors in saccade direction ($> 25\%$).

A two-way repeated measures analysis of variance (ANOVA) with cue validity (valid, invalid) and saccade location (match to target location, mismatch to target location) as factors showed that participants were faster on the validly cued trials than on the invalidly cued trials, $F(1, 9) = 14.81, p < .005$, suggesting that observers covertly allocated their attention to the cued location. Saccades were also initiated faster when the target location and saccade location matched than when they mismatched, $F(1, 9) = 6.49, p < .05$. These data suggest that the allocation of spatial attention automatically results in oculomotor preparation. Covert attention, which was needed to identify the target, engaged the oculomotor system and facilitated saccades to the target location even though there was no incentive to program a saccade. This finding is consistent with the premotor theory of attention (Rizzolatti et al., 1987, 1994). The Cue Validity \times Saccade Location interaction was not significant ($F < 1$), which indicates that maintaining attention at the validly cued location and shifting attention to the uncued location engaged the oculomotor system to a similar extent (see Fig. 2). Although there was no incentive to voluntarily program a saccade to the cued location, mere maintenance of covert attention initiated saccade preparation. When covert attention was switched to the uncued location, in the invalidly cued trials, this switch initiated a similar amount of saccade preparation, although there was no incentive for it.

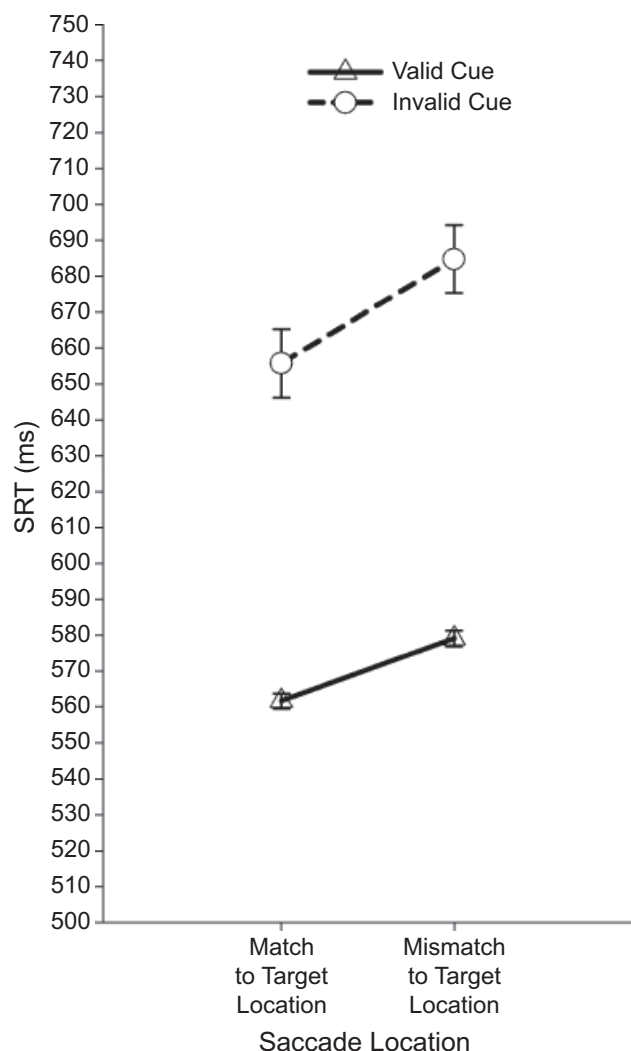


Fig. 2. Mean saccadic reaction time (SRT) on correct trials in Experiment 1 as a function of saccade location and cue validity. Error bars show ± 1 SEM.

To examine the dynamics of the link between covert attention and saccade preparation, we sorted the trials according to whether the target and saccade locations matched on the previous trial. If covert attention always results in saccade facilitation, then one would expect the coupling between covert and overt attention on the previous trial to have no effect on SRT. We analyzed the data with a three-way ANOVA with previous saccade location (match to previous target location, mismatch to previous target location), cue validity (valid, invalid), and current saccade location (match to current target location, mismatch to the current target location) as factors. The effects of cue validity, $F(1, 9) = 15.36$, $p < .005$, and current saccade location, $F(1, 9) = 6.60$, $p < .05$, were significant. In addition, there was a significant interaction between saccade location on the previous trial and saccade location on the current trial, $F(1, 9) = 6.51$, $p < .05$; this finding suggests that the match between the target and saccade locations on one trial had an effect on saccade preparation on the subsequent trial. However, previous

saccade location had no effect on the pattern of attentional allocation (i.e., cuing effect), as it did not interact with cue validity ($F < 1$). No other effects or interactions were significant.

Post hoc analysis showed that a match between the target and saccade location on the previous trial resulted in saccade preparation on the current trial, $F(1, 9) = 15.92$, $p < .005$ (see Fig. 3). This effect was not significantly different for validly and invalidly cued trials ($F < 1$). However, when the target and saccade locations on the previous trial did not match, no saccade preparation was observed ($F < 1$).

On average, participants had a 17% error rate. They made fewer errors in the validly cued than in the invalidly cued condition (14% vs. 20%, respectively), $F(1, 9) = 8.79$, $p < .05$. No other effects or interactions were significant.

The analysis at the intertrial level demonstrates that attention and saccade preparation can be dissociated. The requirement to dissociate covert and overt attention when the target and saccade locations were mismatched abolished saccade preparation on the following trial, while keeping the pattern of attentional allocation intact. This suggests that the coupling between attention and saccade preparation on a given trial influences the coupling of attention and saccade preparation on the following trial. To further explore this hypothesis in Experiment 2, we reduced the probability that the target and saccade locations matched to 25%, thereby increasing the number of trials on which covert attention and saccade preparation had to be dissociated.

EXPERIMENT 2

In order to reduce the probability of a match between the target and saccade locations to 25%, we added two target locations to the lower hemifield in Experiment 2, such that each of the four target locations had an equal probability of serving as a saccade goal. If the coupling between attention and saccade preparation depends on the probability of making a saccade to the attended location, then a dissociation between attention and saccade preparation would be expected. In other words, if the probability of making a saccade to an attended location is low, then no saccade preparation should be associated with allocation of covert attention. In addition, we examined validly and invalidly cued trials to determine whether a dissociation would be observed for both the maintenance and the shifting components of attention. If the acts of maintaining and shifting attention differ in their reliance on the oculomotor system, this difference would be indicated by an interaction between cue validity and saccade location (match, mismatch).

Method

The targets in Experiment 2 were the numbers 1, 2, 3, and 4, and the distractors were the letters H, P, F, and U. Target numbers indicated the location where the saccade had to be made (labeled in a clockwise manner, with 1 referring to the top left, 2 referring to the top right, etc.). As in Experiment 1, the central

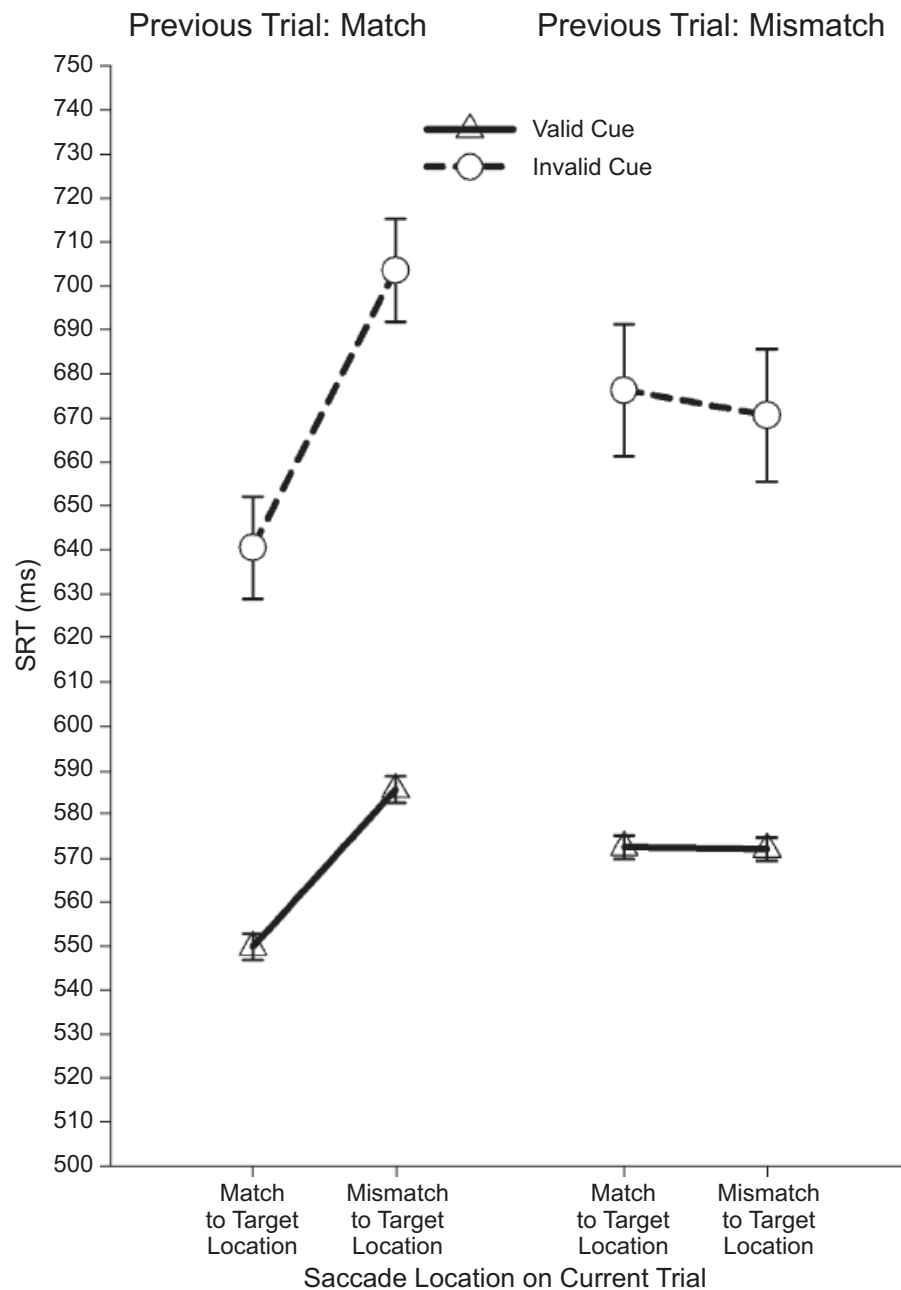


Fig. 3. Mean saccadic reaction time (SRT) on correct trials in Experiment 1 as a function of saccade location on the previous trial (match or mismatch between the target and saccade locations), saccade location on the current trial, and cue validity. Error bars show ± 1 SEM.

cue indicated the target location with 80% probability. For the invalidly cued trials, the location of the target was randomly chosen among the three possible locations. The rest of the experiment was identical to Experiment 1. Thirteen naive participants completed one practice and eight experimental blocks of 40 trials each.

Results and Discussion

Trials with saccades faster than 80 ms or slower than 1,100 ms and trials with saccades that did not start within 1° from fixa-

tion were discarded from further analyses. This resulted in an average loss of 10% of trials. Three participants were replaced because of excessive errors in saccade direction ($> 40\%$).

A two-way repeated measures ANOVA with cue validity (valid, invalid) and saccade location (match to target location, mismatch to target location) as factors showed that saccades were faster on the validly cued trials than on the invalidly cued trials, $F(1, 12) = 34.73$, $p < .001$; this finding suggests that attention was allocated to the cued location. There was no effect of saccade location, $F(1, 12) = 1.6$, $p = .23$, but the Cue Validity

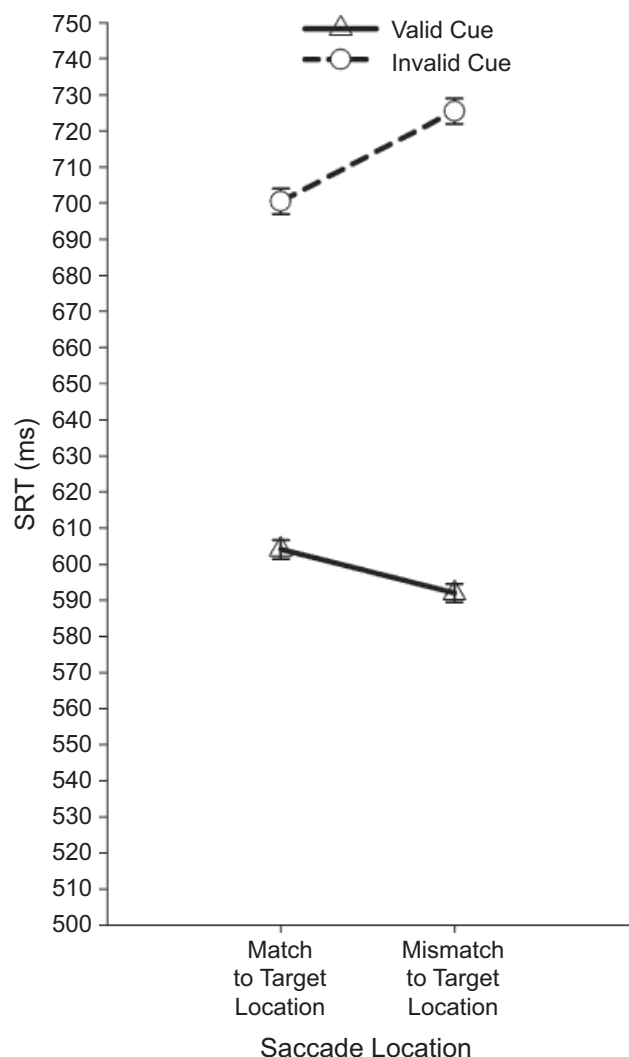


Fig. 4. Mean saccadic reaction time (SRT) on correct trials in Experiment 2 as a function of saccade location and cue validity. Error bars show ± 1 SEM.

\times Saccade Location interaction was significant, $F(1, 12) = 26.27, p < .001$ (Fig. 4). Post hoc analysis showed that for the validly cued trials, initiation of saccades was slower when the target location and saccade location matched than when they mismatched, $t(12) = 2.32, p < .05$. However, for the invalidly cued trials, initiation of saccades was faster when the target location and saccade location matched than when they mismatched, $t(12) = 3.55, p < .005$.

In contrast to Experiment 1, Experiment 2 showed that saccades toward the location where attention was maintained were suppressed (for similar results, see Belopolsky & Theeuwes, 2009; Godijn & Theeuwes, 2004; Klein & Pontefract, 1994). In other words, maintenance of attention at a validly cued location was associated with suppression of saccadic response to that location when the probability of shifting the fovea to that location was low. However, as in Experiment 1, when attention

had to be shifted to an uncued location, saccades to that location were always facilitated.

Further insights were provided by the intertrial analysis. The data were analyzed with a two-way ANOVA with previous saccade location (match to the previous target location, mismatch to the previous target location) and cue validity (valid, invalid) as factors. The effect of cue validity was significant, $F(1, 12) = 26.74, p < .001$. As in Experiment 1, the match between the target and saccade locations on the previous trial had no effect on attentional allocation on the current trial, because it did not interact with the cue validity, $F(1, 12) = 2.43, p = .15$. Planned comparison for the validly cued trials (the number of invalidly cued trials was insufficient) showed that there was a significant interaction between saccade location on the previous trial and saccade location on the current trial, $F(1, 12) = 29.41, p < .001$.

Post hoc comparisons showed that a match on the previous trial resulted in a marginally significant facilitation of saccades to the attended location on the current trial, $t(12) = 1.78, p < .1$, whereas a mismatch on the previous trial resulted in significant suppression of saccades to the attended location, $t(12) = 4.40, p < .005$ (see Fig. 5). The intertrial analysis indicated that the match between the attended and foveated locations on the previous trial had a large effect on the coupling between attention and eye movements: Saccades to the attended location were prepared when there was a match on the previous trial, but were suppressed when there was a mismatch on the previous trial.

On average, participants made errors in 21% of trials. Participants made fewer errors in the validly cued than in the invalidly cued condition (15% vs. 27%, respectively), $F(1, 12) = 14.88, p < .005$. They also made fewer errors when there was a match between the target and saccade locations than when there was a mismatch, $F(1, 12) = 7.31, p < .05$. The Cue Validity \times Saccade Location interaction was also significant for error rates, $F(1, 12) = 10.28, p < .01$. Post hoc analysis showed that fewer errors were made on match trials (20%) than on mismatch trials (34%) in the invalidly cued condition, $t(12) = 3.23, p < .01$, but that there were similar error rates for match trials (15%) and mismatch trials (16%) in the validly cued condition, $t < 1$. This finding indicates the absence of a speed-accuracy trade-off.

GENERAL DISCUSSION

Overall, our results clearly demonstrate that endogenous voluntary attention and saccade preparation can be dissociated. We showed that maintaining attention at a location can either facilitate or suppress initiation of a saccade to that location. The direction of this relationship depends on the probability of making a saccade to the attended location: When this probability is high, the oculomotor system is activated, but when this probability is low, the oculomotor system is suppressed. In addition, the coupling between voluntary attention and eye movement is anticipatory, in that it is strongly influenced by the

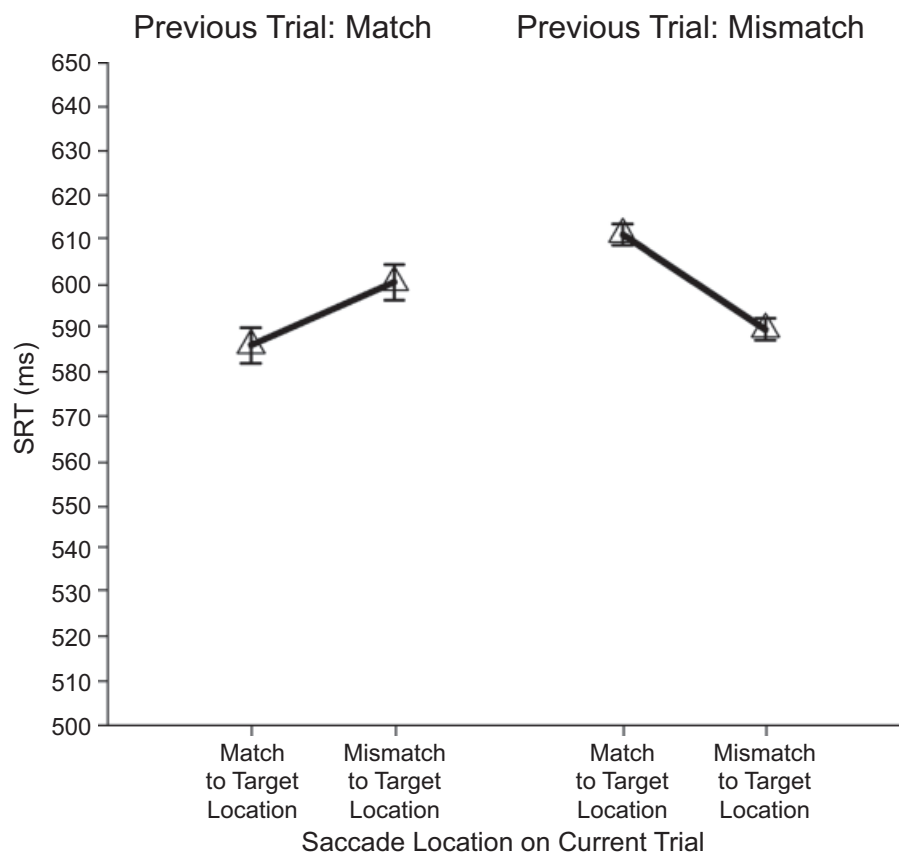


Fig. 5. Mean saccadic reaction time (SRT) on validly cued correct trials in Experiment 2 as a function of saccade location on the previous trial (match or mismatch between the target and saccade locations) and saccade location on the current trial. Error bars show ± 1 SEM.

association formed during the previous trial. Such effects are often considered to be stimulus driven and not under voluntary control (Maljkovic & Nakayama, 1996).

These findings have several important theoretical implications. Coexistence of attentional enhancement and suppression of overt orienting is inconsistent with the classic version of the premotor theory. If allocation of attention is the same as programming a saccade, then allocation of attention would have to be associated with facilitation, not suppression, of overt orienting. However, our results are also inconsistent with the supramodal view of attention. Although we found dissociation between attention and eye movements in the case of attention maintenance, the relationship between these two systems was never neutral. An oculomotor program for a saccade to the attended location was either activated (even when the probability of foveating the attended location was 50%, in Experiment 1) or suppressed (when the probability was 25%, in Experiment 2).

Intertrial analyses also showed that involvement of the oculomotor system was not fixed, but was flexible, switching between activation and suppression, and that effects of saccade location (i.e., a match with the attended location) on the previous trial were found even when the overall probability of coupling

between covert and overt attention was low. This could be the reason why previous studies (Hunt & Kingstone, 2003a; Klein, 1980; Klein & Pontefract, 1994), which examined only averaged effects during maintenance of attention, found independence between attention and eye movements.

In addition, we consistently found that shifts of attention (i.e., on the invalidly cued trials) were associated with saccade preparation. It is plausible that there was simply not enough time to suppress the oculomotor program when covert spatial attention had to be shifted. Our results for the invalidly cued trials are consistent with the premotor theory, showing that orienting of attention to a location is accomplished through activation of a specific oculomotor program. This is why a close relationship between attention and eye movements is typically reported when a shift of attention occurs in close temporal proximity to a saccade (Deubel & Schneider, 1996; Godijn & Theeuwes, 2004). However, the voluntary maintenance of covert attention that occurs after attention is shifted is a somewhat artificial situation. After attention has already been shifted, the oculomotor program can be either maintained (Hoffman & Subramaniam, 1995; Kowler et al., 1995) or suppressed (Belopolsky & Theeuwes, 2009; Klein & Pontefract, 1994), depending on the probability of making a saccade to that location. It might be “uneconomical” (Rizzolatti

et al., 1987) to keep the oculomotor program on-line when the probability of executing it is very low.

To summarize, we obtained clear evidence for a close relationship between the attention and oculomotor systems in a paradigm that allowed simultaneous measurement of the two systems. We propose that the premotor theory of attention has to be updated to include a dynamic component, separating attentional shifts from attentional maintenance. In our view, attention is shifted through the activation of an oculomotor program. However, after attention is shifted, the oculomotor program can be suppressed if the probability of its execution is low.

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REFERENCES

- Abrams, R.A., & Dobkin, R.S. (1994). Inhibition of return: Effects of attentional cuing on eye-movement latencies. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 467–477.
- Awh, E., Armstrong, K.M., & Moore, T. (2006). Visual and oculomotor selection: Links, causes and implications for spatial attention. *Trends in Cognitive Sciences*, 10, 124–130.
- Belopolsky, A.V., & Theeuwes, J. (2009). Inhibition of saccadic eye movements to locations in spatial working memory. *Attention, Perception, & Psychophysics*, 71, 620–631.
- Cavanaugh, J., & Wurtz, R.H. (2004). Subcortical modulation of attention counters change blindness. *Journal of Neuroscience*, 24, 11236–11243.
- Craighero, L., Nascimben, M., & Fadiga, L. (2004). Eye position affects orienting of visuospatial attention. *Current Biology*, 14, 331–333.
- Deubel, H., & Schneider, W.X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, 36, 1827–1837.
- Findlay, J.M., & Gilchrist, I.D. (2003). *Active vision: The psychology of looking and seeing*. Oxford, England: Oxford University Press.
- Godijn, R., & Theeuwes, J. (2004). The relationship between inhibition of return and saccade trajectory deviations. *Journal of Experimental Psychology: Human Perception and Performance*, 30, 538–554.
- Hoffman, J.E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, 57, 787–795.
- Hunt, A.R., & Kingstone, A. (2003a). Covert and overt voluntary attention: Linked or independent? *Cognitive Brain Research*, 18, 102–105.
- Hunt, A.R., & Kingstone, A. (2003b). Inhibition of return: Dissociating attentional and oculomotor components. *Journal of Experimental Psychology: Human Perception and Performance*, 29, 1068–1074.
- Ignashchenkova, A., Dicke, P.W., Haarmeier, T., & Thier, P. (2004). Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. *Nature Neuroscience*, 7, 56–64.
- Juan, C.H., Shorter-Jacobi, S.M., & Schall, J.D. (2004). Dissociation of spatial attention and saccade preparation. *Proceedings of the National Academy of Sciences, USA*, 101, 15541–15544.
- Klein, R.M. (1980). Does oculomotor readiness mediate cognitive control of visual attention? In R.S. Nickerson (Ed.), *Attention and performance VIII* (pp. 259–276). Hillsdale, NJ: Erlbaum.
- Klein, R.M., & Pontefract, A. (1994). Does oculomotor readiness mediate cognitive control of visual attention? Revisited! In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing* (pp. 333–350). Cambridge, MA: MIT Press.
- Kowler, E., Anderson, E., Doshier, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, 35, 1897–1916.
- Maljkovic, V., & Nakayama, K. (1996). Priming of pop-out: II. The role of position. *Perception & Psychophysics*, 58, 977–991.
- Mangun, G.R., Hinrichs, H., Scholz, M., Mueller-Gaertner, H.W., Herzog, H., Krause, B.J., et al. (2001). Integrating electrophysiology and neuroimaging of spatial selective attention to simple isolated visual stimuli. *Vision Research*, 41, 1423–1435.
- Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences, USA*, 98, 1273–1276.
- Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology*, 91, 152–162.
- Muller, J.R., Philiastides, M.G., & Newsome, W.T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Sciences, USA*, 102, 524–529.
- Pashler, H.E. (1989). Dissociations and dependencies between speed and accuracy: Evidence for a two-component theory of divided attention in simple tasks. *Cognitive Psychology*, 21, 469–514.
- Posner, M.I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32, 3–25.
- Posner, M.I., & Petersen, S.E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, 13, 25–42.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25, 31–40.
- Rizzolatti, G., Riggio, L., & Sheliga, B.M. (1994). Space and selective attention. In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing* (pp. 231–265). Cambridge, MA: MIT Press.
- Sheliga, B.M., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental Brain Research*, 105, 261–275.
- Shepherd, M., Findlay, J.M., & Hockey, R.J. (1986). The relationship between eye movements and spatial attention. *Quarterly Journal of Experimental Psychology*, 38, 475–491.
- Smith, D.T., Rorden, C., & Jackson, S.R. (2004). Exogenous orienting of attention depends upon the ability to execute eye movements. *Current Biology*, 14, 792–795.
- Thompson, K.G., Biscoe, K.L., & Sato, T.R. (2005). Neuronal basis of covert spatial attention in the frontal eye field. *Journal of Neuroscience*, 25, 9479–9487.
- Van der Stigchel, S., & Theeuwes, J. (2007). The relationship between covert and overt attention in endogenous cuing. *Perception & Psychophysics*, 69, 719–731.

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